

DORMANCY AND GERMINATION IN *CISTUS CLUSII* (CISTACEAE): EFFECT OF BIOTIC AND ABIOTIC FACTORS

Jorge CASTRO* & Ana Teresa ROMERO-GARCÍA**

RÉSUMÉ

Nous avons analysé des traitements pour améliorer la germination de *Cistus clusii* (Cistaceae), en essayant de simuler les facteurs abiotiques et biotiques propres à l'habitat naturel de cette espèce. L'accroissement des taux de germination est obtenu par scarification chimique (comme celle qui aurait lieu après le passage des graines à travers le tractus digestif des mammifères), et sous un choc thermique similaire celui qui arrive lors des incendies. Dans ce dernier cas, tant l'intensité que la durée d'exposition au traitement sont déterminants.

L'étude de la capacité germinative, après une période de refroidissement des graines, suggère qu'en plus de la dormance imposée par les enveloppes, il y aurait chez cette espèce une dormance physiologique embryonnaire. Ces résultats améliorent les connaissances d'ensemble sur les processus de dormance caractéristiques des semences des Cistaceae.

SUMMARY

An analysis was made of treatments to promote the germination of *Cistus clusii* (Cistaceae), attempting to simulate some abiotic factors (thermal shock) and biotic factors (gibberellic hormones and chemical scarification) of the natural habitat of this species. Germination was increased by chemical scarification (such as may occur when seeds pass through the digestive tract of a mammal) and thermal shock (such as may occur during forest fires). In the latter case, both the intensity and duration of the treatment were determining factors.

The study of the germination capacity after a chilling period showed that, in addition to the dormancy imposed by the seed coats characteristic of the family Cistaceae, in this species physiological dormancy occurs at the embryo level. These results complement the currently available data on the characteristic dormancy processes of Cistaceae seeds, for which dormancy other than that imposed by the seed coats has rarely been described.

INTRODUCTION

Cistaceae is a family of shrubs and herbs which are characteristic of dry, sunny habitats, its main diversification centre being the Mediterranean region

* Departamento de Biología Animal y Ecología (Unidad de Ecología), Facultad de Ciencias, Universidad de Granada, Avda. Fuentenueva s/n, E-18071 GRANADA, Spain. Fax: +34 58 24 32 38. E-mail: jorge@goliat.ugr.es.

** Departamento de Biología Vegetal, Universidad de Granada, Spain.

(Proctor, 1978). All taxa in this family present seeds with hard coats (hardseededness, Thanos *et al.*, 1992), considered to be a particular type of primary seed dormancy (Mayer & Poljakoff-Mayber, 1989) that impedes seed germination unless previous scarification occurs.

In a natural environment, seed scarification can occur in various ways, including fire and animal ingestion (Keeley, 1987; Mayer & Poljakoff-Mayber, 1989; Baskin & Baskin, 1989). After a fire, a strong wave of emergence of Cistaceae seedlings often results (Trabaud & Oustric, 1989a; Roy & Sonié, 1992), and thermal shock in the laboratory promotes seed germination in a number of these species (e.g. Trabaud, 1995 and references cited therein). In addition, the passage of Cistaceae seeds through the digestive tract of animals has been shown to increase germination in this family (Malo & Suárez, 1996).

While dormancy imposed by the seed coat has been widely described in Cistaceae, physiological dormancy at the embryo level has been reported only in rare cases in this family (but see Peña *et al.*, 1988 for a suggestion of secondary dormancy). There are two types of physiological dormancy — primary, physiological dormancy acquired while seeds are maturing in the mother plant; and secondary, dormancy provoked in shed seeds by unfavourable environmental conditions (Mayer & Poljakoff-Mayber, 1989). Physiological dormancy seems to be regulated by temperatures of around 0 °C, affecting the production of hormones involved in the germination process (Bewley & Black, 1994; Vleeshouwers *et al.*, 1995). Thus, traditionally, the most common methods used experimentally to break physiological dormancy have been hormonal treatments and seed stratification (Hartmann & Kester, 1983).

In the present study, we analyse various aspects of germination in seeds of *Cistus clusii* Dunal, a species which, as the rest of the members of Cistaceae, is characterized by hard-coated seeds (Thanos *et al.*, 1992). The objectives of the study were 1) to investigate whether physiological dormancy occurs at embryo level in this species, assuming that in this case a change in the germination percentage after a period of chilling should be expected, and 2) to examine the germination response to treatments intended to simulate common abiotic and biotic factors that act on these seeds in the natural environment. For an abiotic treatment, we applied thermal shock comparable to that produced during a fire, and for biotic treatments, we considered a gibberellic hormone (GA₃) of the type synthesized by embryos, and chemical scarification (sulphuric acid) as may occur in seeds passing through the digestive tract of animals.

MATERIALS AND METHODS

THE SPECIES AND STUDY AREA

Cistus clusii Dunal (Cistaceae) is a shrub reaching 40-70 cm in height, frequently forming part of scrubland vegetation in the western Mediterranean region. It grows in dry, sunny environments, mainly on limestone substrates and in warm habitats, though sometimes reaching altitudes of 1 500 m a.s.l. (Demoly & Montserrat, 1993). This plant is frequent in the southeastern Iberian Peninsula, especially in coastal areas, with moderate levels of both abundance and cover (Martín-Bolaños & Guinea, 1949). The fruit is a woody capsule, 4-8 mm in size,

which opens when ripe, producing 40 to 60 small (about 1 mm thick) seeds released in early autumn. The species is consumed by free ranging-livestock, mainly domestic sheep and goats (Fernández, 1995). Fires are commonly followed by waves of seedling recruitment (personal observation).

For this study, four populations were selected on different hillsides in the province of Granada, southeastern Spain (Table I). The populations, though relatively close to one another (< 50 km apart), range in altitude from sea level to 1 200 m. The climate is of Mediterranean type (Capel-Molina, 1981), but minimum temperatures and precipitation vary according to altitude (Table I). In all four populations, *C. clusii* forms part of a scrubland cover on carbonate substrates. Other common species in the study areas include *Ulex parviflorus*, *Rosmarinus officinalis*, *Thymus* spp. as well as *Genista umbellata* and *Stipa tenacissima* in the three lower populations.

TABLE I

Location of Cistus clusii populations.

Pop. code	Source	Location		Altitude (m)	Mean T. of Jan. (°C)	Prec. (mm)	Date of seed collection
1	Calahonda, Sierra de la Contraviesa	36°43'N,	3°23'W	30	12.4	405	20-VII-94
2	Cerro Gordo, Almuñécar	36°43'N,	3°47'W	50	12.5	474	11-IX-94
3	Lanjarón, Sierra Nevada	36°53'N	3°32'W	600	8.7	511	11-IX-94
4	Sierra de Cázulas	36°50'N,	3°43'W	1 200	- 5.7*	783*	05-IX-94

Note: January is the coldest month. (*), data from a weather station located 180 m higher.

SEED COLLECTION AND GERMINATION EXPERIMENTS

In 1994, ripe fruits were pooled from at least 30 plants per population and each pool was split into two groups, stored in darkness in paper bags either at room temperature of 18 to 25 °C (hereafter, "non-stratified treatment") or refrigerated at a constant temperature of 4 °C (hereafter, "stratified treatment"). Two germination experiments, spanning March and April 1995, were performed in a growth chamber (ASL, ± 0.1 °C) with a photoperiod of 16 h (0600-2200 h) and alternating temperatures of 15 °C during dark periods and 20 °C during light periods. Light was provided by fluorescent tubes emitting a photon flux density of $135 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the PAR range, measured at lamp level using a Li-Cor LI-200 sz pyranometer sensor (Li-Cor Inc., Lincoln, Nebraska, USA). Seeds were placed in glass Petri dishes of 12 cm diameter containing filter paper disks resting on a single layer of 5 mm glass beads (modified from Roy & Sonié, 1992), all materials having previously been sterilized. At the beginning of the experiments, 20 ml of sterilized distilled water was added to each dish, and moisture was replenished as needed (approx. every two weeks). Each Petri dish contained 100 seeds, with 4 replicates per treatment. Dishes were randomly repositioned within the chamber every 5 days. Prior to each experiment, seeds were individually examined under a dissecting microscope, and any damaged or empty seeds were discarded.

Germination, identified as visible radical protrusion, was recorded daily until approx. 95 % of germinable seeds had germinated for each treatment, records being spaced 2-3 days thereafter until complete a 5-week period. The experiments were ended when all treatments registred 10 consecutive days without germination. The germination rate was estimated as T_{50} , i.e. the time needed for manifestation of half of the final germination level. In treatments prone to fungal attack, seeds were previously disinfected by immersion in a 1 % sodium hypochlorite solution for 10 min, followed by thorough rinsing with sterile distilled water.

One experiment was conducted to test the existence of physiological dormancy, and the other to evaluate the impact on germination exerted by treatments simulating the abiotic and biotic factors mentioned above.

Experiment 1. Test of physiological dormancy

We analysed the germination of the stratified and non-stratified seeds for the four populations. Four replicates per treatment and population were used, as described above. At the time of the experiment, stratification had lasted six months for populations 2, 3 and 4, and eight months for population 1. The seeds were disinfected in all cases.

Experimental 2. Effect of abiotic and biotic factors on germination

Non-stratified seeds from population 1 were used, and the following treatment groups were tested:

1. Dry heat in an oven at 100 ± 2 °C for 10, 20, 30 and 60 minutes (treatments Th_{10} to Th_{60}). Seeds were not disinfected.
2. Dry heat in an oven for 10 min at 80, 100, 120 and 140 °C (treatments K_{80} to K_{140}). Seeds were not disinfected. For treatments K_{100} and Th_{10} a single set of four replicates was used, as they represent the same conditions.
3. Immersion of the seeds in a gibberellic acid solution (GA_3) at 50, 100, 200, 400 and 800 ppm for 24 h (treatments G_{50} to G_{800}), keeping the temperature constant at 25 °C. Seeds were disinfected before immersion in the hormone.
4. Immersion of the seeds in concentrated sulphuric acid for 5, 10 or 15 min (treatments S_5 , S_{10} and S_{15} , respectively), keeping temperature of the solution constant at 25 °C. Seeds were immediately rinsed with sterile distilled water, and subsequently disinfected.
5. Controls: we used four additional dishes containing non-disinfected seeds for groups 1 and 2 or disinfected seeds for groups 3 and 4.

The heat treatments fit the range of time and temperature commonly reached by the heat waves at around 2 cm in soil depth during fires in Mediterranean shrublands (Trabaud, 1979; Whelan, 1995), thereby simulating an abiotic factor common in the habitat of the species. Chemical scarification with sulphuric acid erodes the seed coats, increasing their permeability and consequently enhancing germination (Hartmann & Kester, 1983), as happens with seeds passing through the digestive tracts of animals (Mayer & Poljakoff-Mayber 1989; Baskin & Baskin 1989). Thus, this procedure can be considered to simulate of seed consumption by livestock, a biotic factor affecting *Cistus clusii* seeds.

All statistical analyses were carried out with non-parametric tests. Since the sample size was four, the Mann-Whitney test (U values) was used when three or

fewer treatments were involved; for more than three treatments, we used the Kruskal-Wallis test (H values), following Fowler & Cohen (1990). Values are means \pm 1SD. T_{50} values were calculated in days.

RESULTS

EXPERIMENT 1. TEST OF PHYSIOLOGICAL DORMANCY

Chilling affected the seeds from different populations in different ways (Fig. 1). Population 1 revealed no significant differences between the two batches of seeds (8.0 ± 5.7 for stratified seeds and 9.5 ± 2.9 for non-stratified, $U = 10.5$, $p > 0.05$). However, in population 2 the germination percentage of the stratified seeds was lower than that of the non-stratified seeds (1.5 ± 1.0 and 15.3 ± 3.4 respectively, $U = 16$, $p < 0.05$), as in population 3 (6.2 ± 0.9 versus 15.3 ± 2.9 , $U = 16$, $p < 0.05$). Nevertheless, in population 4 (located at the highest altitude; see Table I) the situation reversed, with the stratified batch having the higher germination percentage (11.2 ± 0.9 versus 7.5 ± 1.7 , $U = 15.5$, $p < 0.05$).

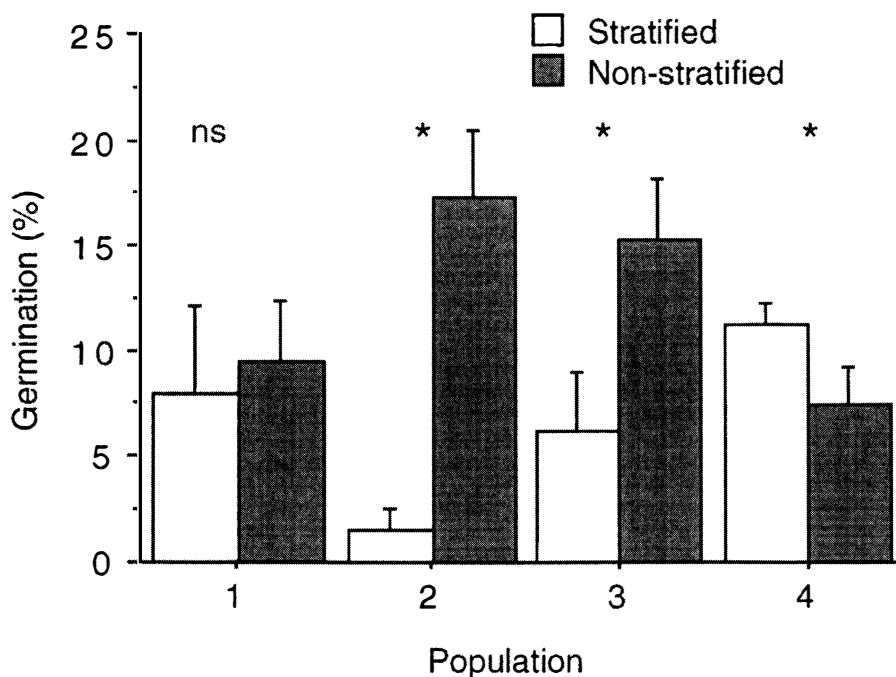


Figure 1. — Germination percentage of stratified and non-stratified seeds for *Cistus clusii* populations. Bars indicate standard deviation. Comparisons within populations were made with a Mann-Whitney test (ns = non significant; * = $p < 0.05$).

EXPERIMENT 2. EFFECT OF ABIOTIC AND BIOTIC FACTORS ON GERMINATION

The germination percentage remained very low unless treatments to promote germination were used. No significant differences in germination percentage were found between the disinfected (9.5 ± 2.9) and non-disinfected (6.5 ± 3.1) control treatments ($U = 12.5$, $p = 0.19$), and T_{50} values were also similar (18 and 19 days, respectively). The percentage of seeds that died during the course of the experiment, was $< 1.5\%$, except for treatment S_{15} (Table II).

TABLE II

Germination percentages and deaths of the treatments applied to Cistus clusii seeds.

Treatment	Germination (%)	T_{50} (days)	Death (%)
Th ₁₀	$31.8 \pm 3.4^*$	18	0.5 ± 1.0
Th ₂₀	$55.5 \pm 2.4^*$	14	0.2 ± 0.5
Th ₃₀	$55.2 \pm 1.0^*$	10	0.0 ± 0.0
Th ₆₀	$47.8 \pm 4.6^*$	12	1.3 ± 1.5
K ₈₀	$14.0 \pm 2.0^*$	17	0.5 ± 1.0
K ₁₀₀	$31.8 \pm 3.4^*$	18	0.5 ± 1.0
K ₁₂₀	$93.2 \pm 2.9^*$	10	1.5 ± 0.6
K ₁₄₀	$71.5 \pm 2.5^*$	10	1.0 ± 1.4
G ₅₀	7.2 ± 1.7^{ns}	10	0.0 ± 0.0
G ₁₀₀	4.8 ± 1.7^{ns}	10	0.0 ± 0.0
G ₂₀₀	9.2 ± 2.6^{ns}	11	0.0 ± 0.0
G ₄₀₀	7.2 ± 1.0^{ns}	10	0.0 ± 0.0
G ₈₀₀	9.5 ± 3.0^{ns}	10	1.0 ± 1.2
S ₅	$41.2 \pm 14.3^*$	5	0.1 ± 0.4
S ₁₀	$63.2 \pm 6.55^*$	4	0.2 ± 0.5
S ₁₅	$49.8 \pm 19.2^*$	5	15.5 ± 12.8

Note: The germination percentages are compared with the percentage obtained for the controls according to the Mann-Whitney test (ns = non significant; * = $p < 0.05$). The \pm value represents the standard deviation. Th, heat of seeds at 100 °C for 10 to 60 min; K, heat of seeds for 10 min at 80 to 140 °C; G, immersion of seeds in gibberellic acid at 50 to 800 ppm; S, chemical scarification by immersion of seeds in sulphuric acid for 5 to 15 min.

Flash heating of the seeds increased the germination percentage in all the cases tested (Table II). When the heat was kept constant at 100 °C and the exposure time was varied (treatments Th), the germination percentage increased in all cases with respect to control. There were differences according to the exposure time ($H = 12.52$, $p = 0.006$). The maximum germination was registered with exposure times of 20 and 30 min (Table II), which gave similar values (55 %). At 10 min, germination increased only slightly (32 %), while at 60 min the germination percentage (48 %) declined significantly in comparison with that recorded at 20 and 30 min ($U = 15.5$, and $U = 16$, respectively; $p < 0.05$). Heating for 10 min at variable temperatures also promoted germination (treatments K, Table II), with differences between the exposure temperatures ($H = 14.26$, $p = 0.003$). The highest

germination percentage resulted from heating at 120 °C (93 %), increasing steadily from 80 °C. However, at 140 °C the percentage decreased (71 %).

The gibberellic hormones did not raise the germination percentage in any of the concentrations tested (Table II). Nevertheless, seeds germinated faster, with T_{50} values of 10 to 11 against T_{50} of 18 for the control treatment, suggesting that the seeds did indeed respond to the hormone. On the other hand, the sulphuric-acid treatments significantly boosted the percentage and rate of germination (Table II). The acid had a scarifying effect by eroding the seed coats, often exposing the cotyledon. The replicates varied widely (reflected in the standard deviation), probably owing to the treatment procedure, since a slight delay in rinsing can cause a considerable variation in the intensity of the treatment because of the highly erosive nature of the acid.

DISCUSSION

TEST OF PHYSIOLOGICAL DORMANCY

As stated above, hardseededness is a common feature in Cistaceae, and other types of seed dormancy have rarely been reported. However, Peña *et al.* (1988) suggested the existence of secondary dormancy at embryo level for *Halimium halimifolium* seeds (Cistaceae). The present study shows that processes of physiological dormancy may also be present in *Cistus clusii* seeds, given the variation in the germination percentage after a chilling period in three of the populations.

A seed without dormancy will germinate, if no other impediment is present, as soon as they find suitable conditions of temperature and humidity, which in the Mediterranean regions typically occurs in spring or early autumn. Physiological dormancy is considered a mechanism that impedes germination during periods when conditions favour germination but not seedling establishment. This type of dormancy appears to be governed by changes in membrane fluidity occurring at temperatures of around 0 °C, affecting the production of hormones involved in the germination process (Bewley & Black, 1994; Vleeshouwers *et al.*, 1995). Thus, in a natural environment, primary physiological dormancy (dormancy entered while seeds are maturing) will prevent germination of seeds during autumn, when seedling establishment during subsequent days is improbable due, for example, to freezing. A period of chilling gives rise to the dormancy-relieving process. In a natural environment this means the end of dormancy during the winter months, allowing seeds to germinate the following spring, an appropriate season for seedling establishment. Even if dormancy is lost before the end of winter, germination will be prevented as low winter temperatures will maintain seed metabolism at minimum until temperatures rise the following spring. Therefore, primary physiological dormancy appears to be more important in populations located at higher altitudes, where winter temperatures are low, whereas in places located at lower altitudes (and therefore with mild winters) primary dormancy may be absent. In population 4, located at the highest altitude and thus with lowest winter temperatures (Table I), the germination percentage increased after a chilling period, suggesting that processes of primary physiological dormancy operate in the seeds of this population. In fact, several studies on the germination capacity of

populations distributed along an altitudinal gradient have shown that seeds from the coldest (highest) sites have a higher degree of dormancy than do seeds from the lowest places, and respond positively to chilling (e.g. Meyer & Kitchen, 1994).

In population 1, chilling had no significant effect, although, in populations 2 and 3, chilling did decrease the germination percentage. Thus, in the latter case, stratification appears to induce secondary dormancy at the embryo level. This situation has been also described for species distributed along an altitudinal gradient — that is, in populations located at medium or lowest altitudes, chilling either causes seeds to enter a process of secondary dormancy or does not change the germination percentage (Meyer & Kitchen, 1994; Meyer *et al.*, 1995). Therefore it seems that *C. clusii* seeds are endowed with mechanisms at embryo level of either primary or secondary dormancy.

EFFECT OF ABIOTIC AND BIOTIC FACTORS ON GERMINATION

The natural germination percentage of *C. clusii* seeds proved to be around 10 % (in contrast to 30-40 % reported by Thanos *et al.*, 1992). However, germination increased with treatments that broke the seed coat.

The maximum germination percentage (93 %) resulted from thermal shock, supporting similar results for other Cistaceae taxa, especially those belonging to the genus *Cistus*, in which germination is promoted by thermal shock at around 80-150 °C (Thanos & Georghiou, 1988; Trabaud & Oustric, 1989b; Roy & Sonié, 1992; González-Rabanal & Casal, 1995; Salvador & Lloret, 1995). This increased germination percentage after thermal shock in *C. clusii* also supports earlier data by Thanos *et al.* (1992), and, furthermore, shows that both the temperature and the exposure time are determining factors in stimulating seed germination, as in other *Cistus* species (Trabaud & Oustric, 1989b). At a fixed time of 10 min, the germination percentage rose as the temperature approached 120 °C, although at higher temperatures (140 °C) the percentage fell, as some seeds were apparently killed by the heat. At a constant temperature of 100 °C, increased exposure time once again boosted the germination percentage to a threshold at which the seeds appeared to die (60 min). The optimal exposure times and temperatures coincide with those measured for the fire-caused heat at a soil depth of around 2 cm (e.g. Whelan, 1995). This may explain the observed wave of germination of *C. clusii* seeds after fires, as occurs in other species of the genus *Cistus* (Trabaud & Oustric, 1989a; Roy & Sonié, 1992). Fluctuations resulting from daily heating and cooling of the soil are considered responsible for the break-down of the coat in hard-coated seeds (Baskin & Baskin, 1989). In this sense, fire-caused heat can be considered an extreme example, provided that seeds lie at an appropriate depth in the soil. Pugnaire & Lozano (1997) have reported fieldwork in which the germination of *C. clusii* seeds was promoted after fire, although they considered soil disturbance to be a more important factor. This study complements those results, but emphasizes the importance of fire-caused heat, suggesting that soil disturbance could have the effect of moving large numbers of seeds into positions within the soil which provide temperatures conducive to germination.

In the treatments simulating biotic factors, gibberellic acid (GA₃) did not increase the germination percentage. However, the germination was faster, indicating that the hormone has an effect on germination but penetrates only those seeds that are not dormant, i.e. seeds with coats sufficiently damaged to enable substances to pass through them.

Chemical scarification by seed immersion in sulphuric acid promoted seed germination up to values of 63 %, and reduced the germination rate to values very close to those reported for mechanical scarification (using sandpaper) with other Cistaceae species (Thanos & Georghiou, 1988). Seed-coat erosion by sulphuric acid is a common method of promoting the germination of seeds with hard coats (Hartman & Kester, 1983). The higher germination percentage after chemical scarification may be advantageous for hard-coated seeds that are eaten by vertebrates, converting the animal into a quantitative and qualitative dispersion vector by virtue of scarification during the digestive processes (Quinn *et al.*, 1994; Malo & Suárez, 1995; Ibañez & Passera, 1997; Campos & Ojeda, 1997). In this sense, livestock (sheep and goats) consume *Cistus clusii* plants (Fernández, 1995), possibly increasing the germination percentage of mature seeds. Indeed, Malo & Suárez (1996) have reported that deer are efficient dispersers of *Cistus ladanifer* seeds, and that the germination percentage increases after the seeds pass through the animals' digestive tracts. This may be extrapolated to other Cistaceae taxa eaten by other ungulates, and Cistaceae hardseededness could be related to animal consumption.

Our results indicate that the dormancy of *C. clusii* seeds is complex, and that mechanism of physiological dormancy may operate. Nevertheless, physical dormancy imposed by the seed coat largely controls germination, and therefore scarifying treatments raise the germination percentage. Thus, indirectly, our data suggest that animals can play an important role in the germination of this taxa. Similar studies in other Cistaceae species could expand current knowledge concerning dormancy and its role in this family.

ACKNOWLEDGEMENTS

We thank the Consejería de Medio Ambiente for permission to sample protected areas. We are also grateful to Regino Zamora, Jose M. Gómez, Jose A. Hódar, and two anonymous reviewers, who gave helpful suggestions that improved the original version. The English version was corrected by D. Nesbitt, and the French abstract was translated by Eva Iñesta. This research was supported in part by a grant from Caja de Madrid Foundation to J.C.

REFERENCES

- BASKIN, J.M. & BASKIN, C.C. (1989). — Physiology of dormancy and germination in relation to seed bank ecology. Pp. 53-66, in: M.A. Leck, V.T. Parker & R.L. Simpson (eds.). *Ecology of soil seed banks*. Academic Press, San Diego.
- BEWLEY, J.D. & BLACK, M. (1994). — *Seeds. Physiology of development and germination*. 2nd. ed. Plenum Press, New York.
- CAMPOS, C.M. & OJEDA, R.A. (1997). — Dispersal and germination of *Prosopis flexuosa* (Fabaceae) seeds by desert mammals in Argentina. *J. Arid Environ.*, 35: 707-714.
- CAPEL-MOLINA, J.J. (1981). — *Los climas de España*. Oikos-Tau, Barcelona.
- DEMOLY, J.P. & MONTSERRAT, P. (1993). — *Cistus*. Pp. 319-337, in: S. Castroviejo, C. Aedo, S. Cirujano, M. Laínz, P. Montserrat, R. Morales, F. Muñoz-Garmendia, C. Navarro, J. Paiva & C. Soriano (eds.), *Flora Ibérica*, vol. III, Madrid.
- FERNANDEZ P. (1995). — *Aprovechamiento silvopastoral de un agrosistema mediterráneo de montaña en el sudeste ibérico. Evaluación del potencial forrajero y la capacidad sustentadora*. Tesis Doctoral. Universidad de Granada.
- FOWLER, J. & COHEN, L. (1990). — *Practical statistics for field biology*. Jonh Wiley & Sons, Chichester.

- GONZALEZ-RABANAL, F. & CASAL, M. (1995). — Effect of high temperatures and ash on germination of ten species from gorse shrubland. *Vegetatio*, 116: 123-131.
- HARTMANN, H.T. & KESTER, D.E. (1983). — *Plant propagation. Principles and practices*. Prentice-Hall (Spanish edition by Compañía Editorial Continental, México, 1987).
- IBAÑEZ, A.N. & PASSERA, C.B. (1997). — Factors affecting the germination of albaida (*Anthyllis cytisoides* L.), a forage legume of the Mediterranean coast. *J. Arid Environ.*, 35: 225-231.
- KEELEY, J.E. (1987). — Role of fire in seed germination of woody taxa in Californian chaparral. *Ecology*, 68: 434-443.
- MALO, J.E. & SUAREZ F. (1995). — Cattle dung and the fate of *Biserrula pelecinus* L. (Leguminosae) in a Mediterranean pasture: seed dispersal, germination and recruitment. *Bot. J. Linnean Soc.*, 118: 139-148.
- MALO, J.E. & SUAREZ, F. (1996). — *Cistus ladanifer* recruitment -not only fire, but also deer. *Acta Oecol.*, 17: 55-60.
- MARTIN-BOLAÑOS, M. & GUINEA, E. (1949). — *Jarales y jaras*. Instituto Forestal de Investigaciones y Experiencias, Madrid.
- MAYER, A.M. & POLJAKOFF-MAYBER A. (1989). — *The germination of seeds*. 4th ed. Pergamon Press, Oxford.
- MEYER, S.E. & KITCHEN, S.G. (1994). — Life history variation in blue flax (*Linum perenne*: Linaceae): seed germination phenology. *Amer. J. Bot.*, 81: 528-535.
- MEYER, S.E., KITCHEN, S.G. & CARLSON, S.L. (1995). — Seed germination timing patterns in intermountain *Penstemon* (Scrophulariaceae). *Amer. J. Bot.*, 82: 377-389.
- PEÑA, J., APARICIO-TEJO, P. & SANCHEZ-DIAZ, M. (1988). — Dormancy mechanism and the effect of scarification in the germination of *Halimium halimifolium* seeds. *J. Plant Physiol.*, 132: 54-58.
- PROCTOR, M.C.F. (1978). — Cistaceae. Pp. 108-109, in: V.H. Heywood (ed.). *Flowering plants of the world*. Oxford University Press, Oxford.
- PUGNAIRE, F.I. & LOZANO, J. (1997). — Effects of soil disturbance, fire and litter accumulation on the establishment of *Cistus clusii* seedlings. *Plant Ecol.*, 131: 207-213.
- QUINN, J.A., MOWREY, D.P., EMANUELE, S.M. & WHALLEY, D.B. (1994). — The “foliage is the fruit” hypothesis: *Buchloe dactyloides* (Poaceae) and the shotgrass prairie of North America. *Amer. J. Bot.* 81: 1545-1554.
- ROY, J. & SONIE, L. (1992). — Germination and population dynamics of *Cistus* species in relation to fire. *J. Appl. Ecol.*, 29: 647-655.
- SALVADOR, R. & LLORET F. (1995). — Germinación en el laboratorio de varias especies arbustivas mediterráneas: efecto de la temperatura. *Orsis*, 10: 25-34.
- THANOS, C.A. & GEORGHIOU, K. (1988). — Ecophysiology of fire-stimulated seed germination in *Cistus incanus* ssp. *creticus* (L.) Heywood and *C. salvifolius* L. *Plant Cell Environ.*, 11: 841-849.
- THANOS, C.A., GEORGHIOU, K., KADIS, C. & PANTAZI, (1992). — Cistaceae: a plant family with hard seeds. *Isr. J. Bot.*, 41: 251-263.
- TRABAUD, L. (1979). — Etude du comportement du feu dans la garrigue de Chênes kermès à partir des températures et des vitesses de propagation. *Ann. Sci. For.*, 36: 13-38.
- TRABAUD L. (1995). — Modalités de germination des cistes et des pins méditerranéens et colonisation des sites perturbés. *Rev. Ecol. (Terre Vie)*, 50: 3-14.
- TRABAUD, L. & OUSTRIC, J. (1989a). — Comparaison des stratégies de régénération après incendie chez deux espèces de cistes. *Rev. Ecol. (Terre Vie)*, 44: 3-13.
- TRABAUD, L. & OUSTRIC, J. (1989b). — Heat requirements for seed germination of three *Cistus* species in the garrigue of southern France. *Flora*, 183: 321-325.
- VLEESHOUWERS, L.M., BOUWMEESTER, H.J. & KARSSSEN, C.M. (1995). — Redefining seed dormancy: an attempt to integrate physiology and ecology. *J. Ecol.*, 83: 1031-1037.
- WHELAN J.R. (1995). — *The ecology of fire*. Cambridge University Press, Cambridge.